II. *On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks. V. On a New Type of Sphenophyllaceous Cone* (Sphenophyllum fertile) *from the Lower Coal-Measures.*

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[Plates 3–5.]

Contents.

Introduction.

One of the most striking results of palæobotanical research has been the discovery that in Palæozoic times a class of Vascular Cryptogams existed, quite distinct from any of the three main groups of Pteridophyta with which we are familiar in the recent flora. This class, the Sphenophyllales, while showing in certain respects a clear affinity with the Equisetales, in other characters rather approaches the Lycopods, and some botanists have endeavoured to trace a relation to the Ferns.* The work of the last few years has pointed to a connection between this extinct group and the recent Psilotaceæ; some authors have gone so far as to include the latter in the Sphenophyllales.† So far as fossil members are concerned, the class is represented by two genera only—the extensive and comparatively well-known genus *Sphenophyllum*, ranging from Devonian to Permian, or, perhaps, Triassic times, and the more recently discovered *Cheirostrobus* from the Lower Carbon-

* Lignier, "Les Sphénophyllales et les Equisétales—leur Origine Filicinéenne commune," 'Bull. Soc. Linn. de Normandie,' 5e Série, vol. 7, p. 93, 1903.

† Scott, "Studies in Fossil Botany," p. 499, 1900; Thomas, "The Affinity of *Tmesipteris* with the Sphenophyllales," 'Roy. Soc. Proc.,' vol. 69, p. 343, 1902; Bower, "Studies in the Morphology of Spore-producing Members," Part V., 'Phil. Trans.,' B, vol. 196, 1903.

iferous,* of which only the fructification is at present known. Each of these genera must be regarded as representing a distinct family within the class. *Sphenophyllum*, indeed, is a "genus" only in name, embracing, if we judge by the fructification, several types of generic value.

The object of the present communication is to describe a newly discovered fossil strobilus, clearly belonging to the family Sphenophylleæ, but presenting new features of considerable importance.†

On April 8, 1904, I received from Mr. JAMES LOMAX three longitudinal sections of a fossil cone, differing from any previously described. The specimen had been discovered by his son, Mr. JOSEPH LOMAX, in a calcareous nodule from Shore Littleborough, Lancashire, a locality in the Lower Coal-Measures, remarkably rich in petrified remains, now being opened up, in the interests of science, by the enterprise of the owner, Mr. W. H. SUTCLIFFE.

The length of the specimen, when found, must have been $2\frac{1}{2}$ inches (60–65 millims.), but the original length of the cone was greater, for it is not complete either at the apex or base. The portion from which the longitudinal sections were cut was about $1\frac{3}{4}$ inches (45 millims.) long. The remaining piece was cut into transverse sections, nine of which pass through the cone, while a couple of others only show small fragments of it. The diameter of the strobilus is about $\frac{1}{2}$ inch (12 millims. or more).

From the general character of the sporangia, which in themselves are much like those of *Sphenophyllum Dawsoni*, and from the obvious dorsiventral segmentation of the sporophylls (Plate 3, phot. 1, and Plate 4, phot. 9), it was at once suggested that the new strobilus was of the Sphenophyllaceous type; the investigation of transverse sections of the axis (phot. 3) soon placed this conclusion beyond doubt, for the anatomy proved to be in all respects that of a young stem of *Sphenophyllum*, scarcely differing from the familiar structure of *S. plurifoliatum*. At the same time the fructification was evidently distinct from that of any known member of the Sphenophyllales, as shown by the absence of any sign of sterile bracts, the closely packed sporangia forming a continuous mass from end to end of the specimen, only interspersed with small appendages, which appeared to be of the nature of sporangiophores. Neither was there any indication of bracts, as distinguished from the sporangiferous laminæ, at the periphery of the specimen. The spores also differed in form from those of any known member of the group. It was thus clear from the first that the Shore strobilus was distinct from any Palæozoic fructification previously described;‡ it appeared to differ in some important characters from its nearest

* SCOTT, "Structure and Affinities of Fossil Plants, etc. On *Cheirostrobus*," 'Phil. Trans.,' B, vol. 189, 1897.

† A short description of the fossil was given before the botanical section of the British Association at Cambridge, in August, 1904.

‡ There was reason to suspect the existence of a new Sphenophyllaceous fructification before the cone

allies, but the extent of the difference could only be determined by more minute investigation. One of the chief points to which attention has been directed is the question whether all appendages of the cone were fertile, or whether we had to do merely with a case of close similarity between fertile and sterile segments, such as we already find, to some extent, in *Cheirostrobus*. The preservation of the specimen is, on the whole, good, and many details are shown in great perfection; at the same time the crowded arrangement and frequent distortion or displacement of the various parts have rendered the interpretation by no means easy. It is much to be hoped that additional and more perfect specimens may soon be discovered; in the meantime it appears desirable to place on record the results already attained, though some points may have to be left undetermined.

General Description.

A general idea of the organisation of the cone is best gained from the most median of the three longitudinal sections. In the upper part of this section (Plate 3, phot. 1) the axis can be traced, with one interruption, for a distance of 17 millims.; below this it is cut off by Stigmarian rootlets, but appears again, lower down, in oblique section. Beyond this the axis is lost, as the section becomes more tangential. In the part where the axis is seen in longitudinal section, four nodes are shown, while a fifth is evidently missing at the point where the first interruption occurs (see phot. 1). At each node the axis is distinctly swollen, as in a vegetative stem of *Sphenophyllum;* the distance from node to node is about 4 millims.; the diameter in the internode appears to have been about 1·8 millims., at the nodes about 2 millims. At the first node (counting from above) no appendages are seen in connection with the axis; the plane of section, which is here somewhat tangential, evidently passes between them. Detached appendages (phot. 1, *d.l.*) (to which we shall return) are, however, shown on either side. Thus the appendages must have been free from each other almost to the base, and there was no disc of coherent bracts as in *Sphenophyllum Dawsoni*.

The second node is important, and affords the best example of the appendages *in situ*. On one side of the node* a double appendage is seen, consisting of a dorsal and a ventral lobe, which separate from one another close to the axis (see also Plate 4, phot. 9). The vertical height of the common base is 1·4 millims.; each lobe where it becomes free has a diameter of almost 0·5 millim. There is no apparent difference between the two lobes, of which the dorsal is directed steeply downwards, the ventral slightly upwards;† the latter is cut off rather shorter than the former. On the other side of the node a single appendage is seen, almost on a

itself was discovered, for isolated sporangia, resembling, but distinct from, those of *Sphenophyllum Dawsoni* had already been observed in the first sections received from Shore Littleborough.

* To the left in phot. 1, to the right in phot. 9. The sides happened to be reversed in photographing.

† The evidence on which the upward and downward directions have been determined is given below.

level with the dorsal limb opposite. The next node preserved—for the intermediate one is lost—shows on the left hand side (phot. 1, *n.* 3) the stumps of both the dorsal and ventral limb, but the plane of section is such that they are cut off very short. On the opposite side the ventral limb can be followed for some distance, though not in median section; the position of the corresponding dorsal lobe is clear, but it is broken off quite at the base.

The remaining node is too incomplete to show the position of the appendages.

The direction of the base and apex of the cone, though not at first sight obvious, can be determined satisfactorily by the course of the bundles or associated tissues at the nodes. Thus, at the second node from above (shown on a large scale in phot. 9), the upward direction of the strand entering the lobe *v.l.* of the double appendage is evident, though the section misses the tracheides; the same holds good for the lobe *d.l.*, where, however, the course of the bundle in which the tracheides are shown is more nearly horizontal. The single appendage on the opposite side of this node does not show the bundle itself, but the trend of the parenchyma is quite evident, and is in the same direction as in the former case. At the first and third nodes, especially the latter (see phot. 1), the direction of the outgoing bundle is also evident, and the collective indications of these three nodes appear to prove decisively that the natural position of the cone was that shown in the photographs.

Practically the whole space between the axis and the periphery of the cone is filled with sporangia, which are large, measuring from 2–2½ millims. in length by about 1½ millims. in breadth. Their arrangement is by no means regular, but on the whole the long axis tends to take a radial direction; where the section becomes tangential the sporangia assume a more isodiametric form. They are filled with oval spores of uniform size throughout the specimen.

Between the sporangia the sections of the appendages are seen here and there—larger and more bract-like towards the axis, but taking the form of slender pedicels as the periphery is approached (Plate 3, phots. 5 and 6; Plate 4, phot. 10, *pd*). At a few places the pedicels are seen in connection with the very characteristic scales or laminæ which form the investment of the cone (phot. 10). The laminæ, which are striking objects owing to the large size of their epidermal cells (phots. 1, 2, 7, 10), bear the sporangia as is shown at many places (phots. 7, 10; Plate 5, fig. 3); there is nowhere any trace of sterile bracts to be distinguished. The laminæ are irregularly arranged—most are peripheral; often they stretch inwards among the sporangia (phots. 1, 10), and in some cases they do not reach the surface at all.

We will now go on to consider the various parts of the cone, and their mutual relations, more in detail, taking the axis first, then the appendages, and finally the sporangia and spores.

The Axis.

The anatomical structure of the axis, especially of the stele, is best shown in one of the transverse sections cut from the upper part of the cone, a short distance above the longitudinal sections (Plate 3, phot. 3). Here the wood is perfectly preserved; its general sectional form is triangular, with somewhat concave sides; each side of the triangle measures about 1 millim.

The primary wood is solid (a fact confirmed by the longitudinal sections (*cf.* Plate 4, phot. 9); its largest elements lie towards the middle, and range from 80–140μ in diameter; the smallest tracheides are, of course, those of the protoxylem at the three angles; these elements may measure as little as 16μ in diameter. Two of the protoxylem-angles are sharp, while the third is more obtuse, but there is no obvious sign of forking; the section is evidently cut through an internode. In the absence of canals at the angles, the axis agrees with that of *Sphenophyllum plurifoliatum*, and differs from those of *S. insigne* and some of the French species described by M. RENAULT.*

A certain amount of secondary wood had been formed, a condition not yet detected in the axis of cones of the *Sphenophyllum Dawsoni* type;† at the sides of the triangle there are only two, or, locally, three ranks of secondary elements; near the angles they are smaller and more numerous, sometimes as many as five in a radial row. The larger secondary tracheides are about 50–60μ in diameter, diminishing towards the angles, where they are nearly as small as the protoxylem-elements. There appear to have been a few parenchymatous cells at the limit between primary and secondary wood.

Longitudinal sections show that most of the tracheides are pitted with numerous, small, bordered pits; the spiral elements at the angles, and intermediate forms of thickening, can be recognised at certain places.

It will be seen from the foregoing description that the structure of the wood is in all respects the same as in a young stem of *Sphenophyllum*, such as *S. plurifoliatum*.

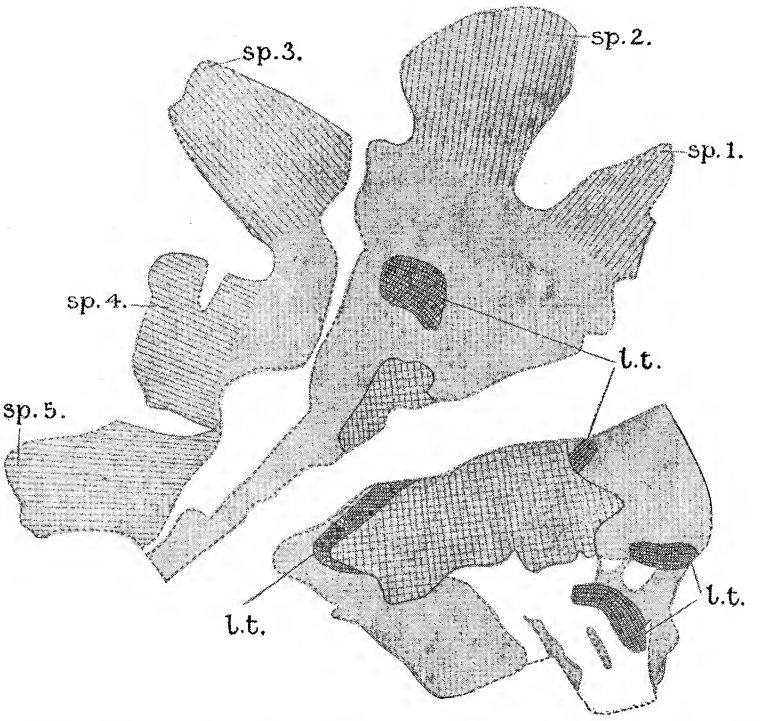
The phloem is not preserved, and scarcely anything remains of the structure of the inner cortex. On two sides the outer cortex is present; the epidermis and the subjacent cortical layers have thick cell-walls, the tissue becoming more delicate towards the interior. The cells, which are often tangentially flattened, are shown by longitudinal sections to be much elongated in the internodes, becoming shorter as the nodes are approached (phot. 9).

Of the other transverse sections, in which the axis is preserved, the most interesting is that shown in text-fig. 1 as it passes through a node, and shows some of the appendages *in situ*. Here the stele is rather larger than in the section already

* 'Cours de Botanique Fossile,' vol. 4, p. 4, Plate A, figs. 1 and 4.

† Secondary xylem occurs, however, occasionally in the axis of *Cheirostrobus*, as shown in some sections of a new specimen which has lately come into my hands. It had previously been found in the peduncle only, where it is well developed.

described, for, as longitudinal sections show, the wood broadened out at the nodes (phot. 9). Five appendages are clearly shown, though broken off rather short. Two of them are in direct continuity with the stem, while the others are severed by an irregular crack passing through the cortex. Another wide crack splits the whole stem in two. The appendages appear to be somewhat connate with each other, as is indicated by the tangential section represented in phot. 4. In any case, they very soon became free, and thus differ widely from the extensive continuous disc formed by



Text-fig. 1.—Transverse section of the axis through a node. The xylem of the stele is shown cross-hatched; the wide crack passes through it. Five leaf-traces (*l.t.*) are shown, two of which are in connection with the stele; *sp.* 1—*sp.* 5, bases of five sporophylls attached to the axis. *Camera lucida* drawing; only the shading is diagrammatic. × 35. S. 2138.

the coherent bracts in the *S. Dawsoni* type, while there is a near approach to the slightly connate condition of the sporophylls in *Cheirostrobus.**

The widest of the appendages (that which is presumably seen in most median section) has a diameter of 560μ where it becomes free. If we must suppose, from the analogy of vegetative stems of *Sphenophyllum*, that the number of appendages in a whorl was some multiple of 3, the choice in this case would lie between 9 and 12, the latter being, perhaps, the more probable, from collateral evidence, though the damaged state of the axis makes it impossible to decide. It is not even certain that, in the fructificative region, we are justified in expecting a multiple of 3. In *Cheirostrobus*, at any rate, as shown by a specimen in the possession of Mr. R. KIDSTON, F.R.S.,

* SCOTT, *loc. cit.*, p. 3, Plates 1 and 2, phots. 2, 6, and 7.

the numbers 10 and 11 occur. The triarch character of the stele in our fossil, however, makes such irregularities less probable.

At the node shown in text-fig. 1, several vascular bundles are present, leaving the stele or traversing the cortex. The exact course of the leaf-traces, however, is obscure, and this is one of the points which must be left open till more favourable specimens are available. The fact that bundles are seen leaving the stele suggests that the section shown in text-fig. 1 was cut rather below the node, and, therefore, that the appendages shown are the dorsal lobes. This is not, however, quite certain, for, from the radial section (phot. 9), it is evident that the bundles of the dorsal and ventral lobes can only have joined quite close to the stele, and it is even possible that they may have sprung from it independently.

The relative number and position of the dorsal and ventral lobes could not be determined. At the node shown in detail in phot. 9, the ventral and dorsal lobes of the sporophyll to the right appear to be placed almost vertically one above the other. The dorsal is, however, cut rather more medianly than the ventral lobe. On the opposite side only one lobe is shown, which seems from its position to be the dorsal one; there is no sign of any ventral lobe;* its apparent absence, which obliquity of the section appears inadequate to explain, may show that the two sets of lobes were not regularly superposed. Unfortunately, none of the tangential sections solve this difficulty.

We may recapitulate as follows the chief points established so far.

1. The axis contains a triarch stele, with solid wood and slight secondary growth. In all respects its anatomy agrees with that of a stem of *Sphenophyllum*.

2. The axis bears whorled appendages, free from one another except at the base, where they are slightly connate.

3. The appendages divide into dorsal and ventral lobes, which appear to be similar to one another.

The Appendages.

The appendages of the axis are much broken and displaced, and can never be traced through anything like their whole extent. Hence it is necessary to reconstruct them as well as we can from the somewhat fragmentary evidence available. We have already considered their relation to the axis, and will now endeavour to follow their course to the periphery of the cone.

The section shown in Plate 3, phot. 4, is a tangential one, passing through part of a verticil close to the axis. Three connate appendages are shown, two of which are fairly complete; each of the latter contains a vascular bundle; the one to the right is cut furthest to the outside. The verticil is uninjured below, while its upper edge

* A somewhat ill-preserved body lying against the upper side of this appendage might possibly be interpreted as the missing ventral obe; in any case it does not affect the question, as it is certainly not *in situ*.

is irregular and broken; consequently the appendages seen must be dorsal lobes, while the corresponding ventral portions are lost.

Where the plane of section cuts a verticil a little further out, similar sections of appendages are met with, but here they have become free from one another. An example of this is shown in phot. 5, where two such appendages are seen in transverse section—they measure about $560 \times 320\mu$. The former dimension agrees with the width of the appendages seen *in situ* in the transverse section (text-fig. 1). The appendages are almost semi-circular in section; their tissues are fairly well preserved, and consist of an epidermis enclosing rather thick-walled parenchyma, traversed by a vascular bundle which lies a little nearer the upper than the lower surface; the xylem is surrounded by a gap where the softer tissue has decayed. Perfectly similar bodies are seen in oblique section close to the uppermost node shown in phot. 1, *d. l.*; they clearly represent the dorsal lobes of the verticil springing from this node. This, then, gives us the structure of the dorsal limbs of the appendages, where they first become free; it is an important question whether the structure of the ventral lobes was the same. It is, however, extremely difficult, in a tangential section, to distinguish between the two. Thus the appendages shown in phot. 5, from a tangential section of the cone, probably represent dorsal lobes of the whorl belonging to the uppermost node seen in the radial section (phot. 1); they may, however, be ventral lobes of the next whorl below. The appendages appear pretty frequently in the tangential sections, and where three or more successive series are shown, one above the other, it is evident that both dorsal and ventral lobes must be represented. No material difference in form or structure could be detected, where the appendages appear to be cut at about the same distance from the axis. We may conclude, then, that the structure of both dorsal and ventral lobes in the region near their base was essentially that shown in phot. 5.

The appendages were branched, as is clearly shown at many places in the preparations. An example of this is illustrated in phot. 6, where two segments springing from a common base are shown. The basal part has a diameter of about 0·5 millim., while the segments are somewhat tapered, diminishing from 240 to 160μ in diameter. A vascular bundle is seen in the common base, and reappears in the right-hand segment, where it can be followed for some distance. Another bundle is shown at the end of the other segment, at the point where it is seen in approximately transverse section beyond the sharp bend. This cannot be a case of the dorsiventral division of a main appendage, for the dimensions throughout are much too small (*cf.* pp. 19 and 22); it can only represent the further subdivision of either a dorsal or ventral lobe. Though only two segments are shown here, there may have been more in reality; at any rate, we find them more numerous in other cases. Thus the appendage represented in Plate 5, fig. 1, from a transverse section of the cone, clearly had four segments, three of which are evident as such, while the remaining one (*sg.* 3) is chiefly indicated by its vascular bundle. The plane of section in this case appears to

be nearly, though not quite, parallel to the surface of the organ, indicating that the plane of branching of the appendages was approximately transverse to the axis of the cone, as is further shown by tangential sections. In other cases, also, appendages with three or four branches are shown.

The branches or segments into which the lobes divide appear to be identical with the sporangiferous pedicels; there is no evidence of any further ramification. Although there is no case in which the pedicels can be traced continuously through their whole length, there are several instances of pedicels seen in connection with the fertile laminæ; they are evidently identical with the segments of appendages, such as phot. 6 represents. An interesting case is shown in the radial section of the cone (see Plate 3, phot. 1, for general view, and Plate 4, phots. 9 and 10, for details).* The dorsal lobe of the double appendage at the second node from above, can be followed for a distance of about 2 millims. from its base; here it is interrupted, apparently by some injury. But exactly in the line of its outward prolongation we come to a pedicel attached to a lamina which bears a sporangium (phot. 10, *pd;* see description of Plates). Between the pedicel and the dorsal lobe is a detached fragment (*a*) thicker than the pedicel, which presumably formed part of the same appendage. The inference is very strong that the pedicel is a branch of the dorsal lobe to which it corresponds, and consequently that the dorsal lobes were fertile, terminating in the sporangium-bearing laminæ. In a position roughly corresponding to the ventral lobe of the same sporophyll there is another pedicel attached to a lamina just like the former, though not actually showing a sporangium in connection. Here, also, there are intermediate fragments of an appendage. The evidence suggests that both dorsal and ventral lobes of the sporophylls were fertile, a condition not hitherto met with among the Sphenophyllales. A careful examination of all the sections appears to raise this conclusion to a certainty. Nowhere is there any trace of sterile bracts, everywhere the appendages are similar, and all alike terminate, wherever they can be traced, in similar sporangium-bearing laminæ. It is this character which has suggested the name—*Sphenophyllum fertile*—proposed for the new species.

We will now go on to consider the fertile laminæ more in detail. The most usual position of the laminæ is at the periphery of the cone, of which they formed the sole external investment (phots. 1 and 2). At several places, however, laminæ are met with which do not reach the surface, but lie embedded among the sporangia (as in the section S. 2133). Even where the laminæ extend to the periphery, their position is very variable, and they sometimes lie almost in a radial direction (phot. 2). Such irregularities may be due to accidental displacement, but the natural arrangement was probably less rigid than in *Sphenophyllum Dawsoni*, or the almost geometrically regular *Cheirostrobus*.

The form of the lamina has, of course, to be inferred from the comparison of various sections. Where it is seen in its full extent it usually subtends two

* As already mentioned, the right- and left-hand sides are reversed in the general and detailed views.

sporangia; cases of this kind are frequent, and occur both in transverse and longitudinal sections—an example from each is figured (see Plate 3, phot. 7, from a transverse, and Plate 5, fig. 3, from a longitudinal section). The maximum length of the lamina, as shown in sections of this kind, is 3·5 millims.; other similar sections may measure as little as 2 millims., but are probably cut obliquely. Sections in which the lamina appears still narrower (1–1·5 millims.) are evidently cut transversely to it; such sections either miss the insertion of the sporangia altogether, or, at most, show only one of them in position (see Plate 5, fig. 2). It thus appears that the form of the lamina was oblong or oval, and not isodiametric, a conclusion confirmed by sections approximately parallel to its surface (see Plate 5, fig. 5). The pedicel was, no doubt, attached about the middle of the lamina, though no section has been found showing in one view the pedicel and the two sporangia in connection with the lamina. The insertion of the pedicel and of one sporangium are clearly seen in Plate 4, phot. 10, but the lamina is not shown in its full extent, and the other sporangium is missed. The position of the various parts of the sporangiophore is, however, well seen in phot. 11, representing a section cutting the whole organ in a nearly tangential, though somewhat oblique plane, which passes partly through the lamina, and partly through the sporangia belonging to it. In the middle of the group is the pedicel (*pd*), seen in transverse section; the upper sporangium (as the figure is placed) is cut across in its full extent; below, the section passes through a portion of the lamina (*lm*), and also through the base of the second sporangium. The body (*lm'*) between the two sporangia on the right-hand side of the figure is probably a part of the edge of the lamina, which was here sufficiently incurved to meet the plane of section.

The arrangement of the parts in this section clearly indicates that only two sporangia were borne on the lamina, and this was, no doubt, constant. There is never any trace of more than two, and as the sections cut the laminæ at all angles, indications of others must have been met with if a larger number had been present. The elongated form of the lamina also points to its being bisporangiate. The fact that laminæ showing two sporangia appear both in transverse and longitudinal sections, might have led to the inference that there were four in all, as in *Cheirostrobus* or *Calamostachys*, if they appeared at all constantly in both planes. This, however, is not the case; it is rather the exception, in each plane of section, for the two sporangia to appear, while narrow sections of laminæ showing only one sporangium, if any, are frequent. Thus all indications point to the conclusion that the sporangiophores each bore two sporangia, and no more, as in the *Bowmanites Römeri* of Count Solms-Laubach.

The structure of the laminæ is very characteristic. The external epidermis, commonly, though not always, coinciding with the periphery of the cone, is a conspicuous, large-celled layer, forming a striking feature in all the sections (see phots. 1, 2, 7, etc.). These cells measure 300μ or more in radial diameter, and about

100–180μ in the tangential direction (see Plates 3 and 4, phots. 7, 10 and 12; Plate 5, figs. 2, 3, and 4). When seen in surface-view, they appear roughly isodiametric (Plate 5, fig. 5). Their cell-membranes are moderately thickened, especially on the external and lateral walls (Plate 5, figs. 2 and 4). At the edges of the lamina, where the outer passes over into the inner epidermis, there is a marked diminution in the size of the cells (Plate, 5, fig. 2; Plate 4, phot. 12); those of the inner epidermis are quite small, often only about 24μ in depth and width, though sometimes considerably elongated in the direction of the long axis of the lamina. The delicate tissue of the mesophyll is imperfectly preserved. A vascular bundle entered the lamina from the pedicel (see Plate 4, phot. 10), and its general course is evident, though not shown completely in any one section. It forked on entering the lamina, and the two branches traversed it longitudinally in opposite directions, each terminating at the base of a sporangium (see Plate 5, fig. 4). Sections of the lamina show the bundle at all points of its course. In transverse sections, such as that represented in fig. 2, Plate 5, the bundle itself is cut transversely; the plane of this section appears to have lain between the pedicel and one of the sporangia. It also appears in transverse section in phot. 12, but here the lamina is cut across close to the base of a sporangium, as shown by comparison with longitudinal sections (*e.g.*, Plate 5, fig. 4), and with sections passing through the sporangium itself at its base (phot. 13). The relation of the bundle-ending to the sporangium is very similar to that in *Sphenophyllum Dawsoni*.*

The connection between lamina and sporangium is well shown at various places (see Plate 3, phot. 7, and Plate 5, figs. 3 and 4). The external wall of the sporangium (figs. 3 and 4) is directly continuous with the outer epidermis of the lamina, exactly as the corresponding sporangial wall in *S. Dawsoni* is continuous with the "crest." The transition from the epidermis to the sporangial wall is marked by a diminution in the size of the cells, and by the appearance of the buttresses on the cell-walls, which are characteristic of the sporangia, as in *Sphenophyllum* and *Cheirostrobus*, and also in *Calamostachys* and other Calamarieæ (see Plate 5, fig. 5). The mesophyll of the lamina runs out into a pad of delicate tissue, which occupies the base of the cavity of the sporangium, and dies out gradually along its walls (Plate 5, fig. 4; Plate 4, phots. 12, 13, and 14). The vascular bundle comes to an end before actually entering the sporangium.

On the inner side (*i.e.*, on that turned towards the fellow-sporangium) the sporangial wall meets the lower epidermis of the lamina at an acute angle, so that the limit between the two is indicated by a sharp constriction (fig. 4). The character of the sporangial wall in this part depends on the plane of section. It may have a marked shoulder, consisting of large cells without buttresses, resembling those of the

* WILLIAMSON, "Organisation of Fossil Plants of Coal-measures," Part XVIII., 'Phil. Trans.,' B, vol. 182, 1891, Plate 27, fig. 16; WILLIAMSON and SCOTT, "Further Observations on the Organisation of Fossil Plants, etc.," Part I., 'Phil. Trans.,' B, vol. 185, 1894, Plate 85, fig. 58.

outer epidermis of the lamina (fig. 4), or it may pass at once to the smaller buttressed cells of the ordinary sporangial wall (phot. 7). Transverse sections of the sporangium throw some light on these different appearances. In phot. 13 one of the sporangia from the group in phot. 11 is shown, cut across close to the base; the whole of the cavity exposed by the section is filled with the delicate tissue of the basal region, but the vascular bundle has already died out. On one side the wall is cut almost tangentially, and here it consists of two prominent lobes with a deep furrow between them. The lobes evidently correspond to the prominent shoulder seen in the longitudinal section (Plate 5, figs. 3 and 4); their cells are large, and without buttresses, while nearer the furrow small buttressed cells are present; on the opposite side of the sporangium, where the wall is seen in section, the cells are large, but show some buttresses. We thus see that the appearance shown in fig. 4 is due to the plane of section passing through one of the large-celled lobes. When cut nearer the median plane the wall may show buttressed cells throughout (Plate 3, phot. 7).*

The structure of the pedicel is remarkably like that in *Sphenophyllum Dawsoni* and *Bowmanites Römeri;* in all three species the epidermal cells are conspicuously enlarged on the side of the pedicel directed outwards (see phots. 11 and 13).† In our fossil, as in *S. Dawsoni*, this peculiarity is most marked in the upper expanded part of the pedicel, though it begins to appear lower down (see Plate 3, phot. 6, at the point where the pedicel is seen in nearly transverse section). The bundle of the pedicel, as shown in Plate 4, phot. 13, appears to be collateral, but this is a point on which I have not been able to satisfy myself. The tracheides, both in pedicel and lamina, are for the most part densely spiral, sometimes reticulated.

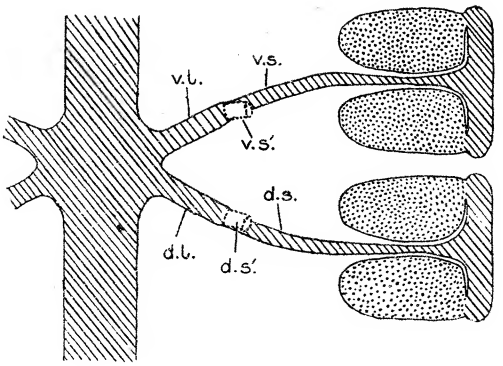
We may now recapitulate the chief conclusions we have reached as regards the appendages of the strobilus :—

1. Both dorsal and ventral lobes of the sporophyll were fertile.
2. Each lobe divided in a palmate manner into several (sometimes four) segments —the sporangiophores.
3. Each sporangiophore consisted of a slender pedicel, expanded at the distal end, and bearing an elongated, peltate lamina.
4. The lamina bore two pendulous sporangia attached at its margins.
5. The vascular bundle traversing the pedicel divided on entering the lamina, each branch terminating at the base of a sporangium.

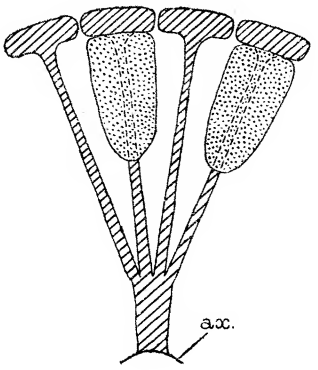
The accompanying diagrams (text-figs. 2 and 3) will serve to make clear the essential points in the morphology of the sphorophyll.

* In order to understand the structure of the base of the sporangium, it is necessary to compare the three transverse sections shown in phots. 12, 13, and 14, with the longitudinal section shown in fig. 4, on which the planes of the corresponding transverse sections are approximately indicated.

† *Cf.* WILLIAMSON and SCOTT, "Further Observations, I.," 'Phil. Trans.,' B, vol. 185, 1894, Plate 85, fig. 57; SOLMS-LAUBACH, "*Bowmanites Römeri*," 'Jahrbuch d. K.K. Geolog. Reichsanstalt,' 1895, Taf. X., fig. 10.



Text-fig. 2.—Diagram of a node in longitudinal section, showing one sporophyll, and the base of the opposite one. *v.l.*, ventral lobe of the sporophyll; *v.s.*, one of the segments or sporangiophores into which it divides, terminating in a peltate lamina bearing two sporangia; *v.s.'*, stump of another segment; *d.l.*, dorsal lobe; *d.s.*, one of its segments, like *v.s.*; *d.s.'*, stump of another segment.



Text-fig. 3.—Diagram of a single sporophyll, as it would appear in a transverse section of the cone, so that only one lobe (either dorsal or ventral) is seen; *ax.*, part of axis to which sporophyll is attached. The lobe divides into four segments or sporangiophores, each terminating in a lamina; all the laminæ are shown in the plane of their shorter diameter. In two, the section is median, passing through the pedicel, while the alternate two are shown in end-view, so that one of the sporangia is seen in each case.

In text-fig. 2 both laminæ are shown the long way (parallel to their longer diameter); in text-fig. 3 all are shown the short way. In reality their positions appear to be quite irregular (see p. 25). Both diagrams are drawn roughly to scale and × about 7.

The Sporangium.

Some points in the structure of the sporangia have already been mentioned, in describing their insertion on the sporangiophores. The wall of the sporangium, as preserved, is one cell thick, except at the base, where, as we have seen, there is an internal lining tissue of considerable thickness, which thins out, and soon disappears, as we reach the spore-containing cavity (Plate 5, figs. 3 and 4; Plate 4, phot. 14). The lining tissue consists of thin-walled cells, elongated in the direction of the long axis of the sporangium.

The actual wall of the sporangium consists of three different kinds of cells :—

1. The large cells of the two prominent lobes near the base.
2. The buttressed cells, forming the greater part of the wall.
3. Narrow cells without buttresses, forming a longitudinal band coincident with the furrow between the lobes, and apparently constituting a *stomium*.

The large cells (1) (Plate 4, phot. 13 ; Plate 5, figs. 4 and 7) have a radial depth of about 200μ ; as already mentioned, they resemble the cells of the external epidermis of the lamina, with which they are continuous at the back of the sporangium (fig. 4), but are rather more elongated, as seen in surface-view. The buttressed cells (2), constituting the greater part of the wall, have a depth of about 80–100μ. Seen in surface-view (phots. 8 and 13) they appear more or less rhomboid, and elongated in the direction of the long axis of the sporangium ; their length ranges from 140–200μ, and their width from 50–110μ. The lateral walls of the cells are slightly undulating, and are provided with buttresses, or vertical ridges, projecting from the wall into the cavity of the cell (Plate 3, phot. 8). When the sporangial wall is seen in a section approximately parallel to its long axis (*e.g.*, Plate 4, phot. 10 ; Plate 5, fig. 3) the buttresses mostly appear as sharp lines, vertical to the surface, simulating septa, but with less depth on focussing, and often incomplete where they pass out of the plane of section (fig. 6, A). In transverse sections of a sporangium, the buttresses may be seen in side-view, projecting from the septa (Plate 5, fig. 6, B).* The whole arrangement is quite similar to the well-known structure of the sporangial wall in *Calamostachys*,† *Cheirostrobus*,‡ and other strobili of the Calamarieæ and Sphenophyllales. A band of small cells (3) runs lengthways of the sporangial wall, starting at the base of the sporangium, and passing between the large-celled lobes (phot. 13, *st*) ; in this part it lies at the bottom of a deep furrow, which is already well marked at a level where the vascular bundle is still seen, and where we may therefore regard the section as still belonging to the lamina rather than to the sporangium (Plate 4, phot. 12, *st*). Above the basal region the furrow becomes less conspicuous (Plate 5, fig. 6, A). When the band is seen in surface-view, we find along its median line two or three rows of very small, square, rather thick-walled cells only about 20μ in diameter, and without buttresses (Plate 3, phot. 8). Their depth, as seen in section, is about 30μ (Plate 5, fig. 6, A, *st*). On either side of the small-celled strip somewhat larger elements are present, which form the transition to the typical buttressed cells of the rest of the wall (Plate 3, phot. 8). In sections near the base of the sporangium, the small cells at the bottom of the furrow have sometimes split apart, as if dehiscence had already taken place (Plate 4,

* It is, however, very much a matter of chance which view is obtained.

† WILLIAMSON and SCOTT, "Further Observations, etc.," Part I., 'Phil. Trans.,' B, vol. 185, 1894, p. 909, Plate 81, fig. 31 ; WEISS, 'Steinkohlen-Calamarien,' vol. 2, 1884, Plate 23, fig. 2, Plate 24, figs. 3, 4, and 5.

‡ SCOTT, "*Cheirostrobus*," *loc. cit.*, 'Phil. Trans.,' B, vol. 189, 1897, p. 13, Plate 5, fig. 13.

phot. 14, *st;* and Plate 5, fig. 7, *st*), while in other places their connection is still unbroken (fig. 6, A, *st*). It seems clear that the small-celled band is to be regarded as the *stomium* through which the line of dehiscence ran.

From the comparison of the transverse section shown in Plate 4, phot. 12, with the longitudinal section in Plate 5, figs. 3 and 4, it appears that the stomium lay on the *inner* side of each sporangium, *i.e.*, on the side towards its fellow. The sporangium shown in phots. 11 and 13 must thus have been somewhat displaced.

The structure of the side of the sporangial wall where dehiscence took place, is strikingly similar to the corresponding part in *Lycopodium clavatum*, as figured by GOEBEL;* in that plant, as in our fossil, the cells of the wall are for the most part provided with buttresses, while the narrower cells of the stomium are nearly or quite destitute of them. The difference in size between the cells of the stomium and their neighbours is not, however, so extreme in the recent as in the fossil sporangium.

The bilobed group of enlarged cells at the basal end of the sporangium appears not to be represented in Lycopodiaceous sporangia; it may not improbably have acted as an annulus, analogous to the group of modified cells which represents the annulus in the Osmundaceæ.

The sporangia of the Sphenophylleæ were evidently highly differentiated organs, fully equalling in complexity those of any living Pteridophyte. The structure of the sporangium of *Sphenophyllum Dawsoni*, which has not yet been completely elucidated, appears to be essentially similar to that of our species.

The chief results arrived at from the investigation of the sporangia may be recapitulated as follows:—

1. The sporangial wall, which is one cell thick, except at the base, consists for the most part of buttressed cells, like those in *Calamostachys* or *Cheirostrobus*.

2. At the base of the sporangium there is a double group of larger wall-cells, for the most part without buttresses, which may have acted as an annulus.

3. The line of dehiscence was longitudinal, and is marked by a band of very small cells, without buttresses (the *stomium*), running the whole length of the sporangium, along its inner side.

The Spores.

All the sporangia of the cone contain numerous spores (phots. 1, 2, 7, 10, etc.); the specimen had no doubt been accidentally detached from the plant before normal dehiscence had taken place, though a few spores may have escaped by subsequent rupture of the sporangial walls.

Throughout the specimen all the spores are of one kind. They are of ellipsoidal shape, measuring 90–96μ in length by 65–70μ in width (see Plate 5, figs. 8–11).

Two layers can be distinguished in the spore-membrane—the outer thick and dark, the inner much more delicate, and usually contracted (Plate 5, figs. 8 and 10). The

* "Organographie der Pflanzen," p. 753, fig. 496, 1901.

sculpturing of the exospore is characteristic; it bears several (about five) sharp ridges or crests, approximately parallel to each other, and running round the spore in the direction of its major axis like lines of latitude on a globe (fig. 11). The crests are thin plates, vertical to the surface, as is seen when they appear in section (figs. 8 and 9). Where the spore is cut parallel to the course of the crests, a surface-view of the latter is obtained, the crest appearing as a delicate rim at the edge of the spore (fig. 10). I have not succeeded in detecting any serration of the margin or ribbing on the surface of the crests, such as occur on the wings of the spores in *Sphenophyllum Dawsoni* and *Bowmanites Römeri*, but the roughnesses which appear on the crests when seen edgeways (fig. 12) may indicate some similar structure. In the thin sections the surface of the spore-wall has often been sliced off, so that the crests alone are seen, connected, perhaps, by a fragment of the outer membrane (fig. 12). In some cases anastomosis occurs between adjacent crests (fig. 12). We thus see that, both in form and sculpturing, the spores of *Sphenophyllum fertile* differ from those of any species previously described.

Summary.

1. The strobilus was the fructification of a *Sphenophyllum*, as shown by the anatomy of the axis, which is identical with that of a young *Sphenophyllum*-stem, and by the division of the whorled sporophylls into dorsal and ventral lobes.

2. The number of members in a verticil appears to have been from nine to twelve. The verticil was polyphyllous, or nearly so, the sporophylls being only slightly connate at the base.

3. Both dorsal and ventral lobes of the sporophylls were fertile, and no sterile appendages have been met with. Each lobe divided into several segments (in some cases four), the sporangiophores.

4. The sporangiophore consisted of a slender pedicel, terminating in an oblong, peltate lamina, which bore two pendulous sporangia. The vascular bundle of the pedicel divided into two strands, running to the bases of the two sporangia.

5. The sporangial wall consisted for the most part of buttressed cells, as in *Calamostachys*, with a double group of larger cells at the base. The dehiscence was longitudinal, by means of a well-defined stomium.

6. The spores, so far as observed, were all of one kind; they are ellipsoidal in form, with longitudinal ridges.

In the above summary, paragraphs 3, 4, and 6 will suffice for the purpose of a diagnosis of the species *S. fertile*.

Affinities.

As already pointed out, both the morphological and anatomical characters of the strobilus indicate that it is most naturally to be referred to the genus *Sphenophyllum*, as at present constituted. The dorsiventral division of the whorled

sporophylls, the structure of the sporangiophores and sporangia, and the anatomy of the axis collectively suffice to justify this reference. The genus will, no doubt, eventually have to be broken up, as our knowledge of the organs of fructification increases, and we become better able to correlate them with the vegetative parts; the time is hardly ripe for such a rearrangement at present.*

A number of fructifications referable to *Sphenophyllum*, or at least closely allied, have now been described; the most important are *Sphenophyllum Dawsoni*, *Bowmanites Römeri*, and *Sphenophyllum majus*. Of these, *Bowmanites Römeri* appears to have most in common with our fossil. This fructification, our knowledge of which is entirely due to the work of Count Solms-Laubach,† was not definitely placed by that author in the genus *Sphenophyllum*, though there is no doubt as to its close affinity. As the structure of the axis is not yet known, it is wise to keep this species at present in the provisional genus *Bowmanites*.‡ The fact that in *B. Römeri* each sporangiophore bears two sporangia is in itself a striking point of resemblance to *Sphenophyllum fertile;* in the detailed structure of the fertile lamina and the mode of attachment of the sporangia there is also a fairly close agreement. Count Solms-Laubach finds that in his species the pendulous sporangia were inserted far to the outside on the lower edge of the expanded summit of the sporangiophore.§ He compares their position with that of the ovules in *Zamia* or *Encephalartos*.‖ This description holds good equally for *Sphenophyllum fertile*, and the course of the bundles supplying the sporangia seems also to have been identical in the two cases.¶ The pedicel in *B. Römeri* is described as having enlarged epidermal cells limited to its outer side, just as in our fossil,** while the large-celled external epidermis of the lamina (*Schuppe*) is similar to, though more strongly developed than in the lateral enlargements of the wall which occur near the base of the sporangium,†† a description which might have been taken from *Sphenophyllum fertile*. The fact that the bracts of *B. Römeri* are free nearly to their base‡‡ is also a point of resemblance to the appendages of our strobilus.

On the other hand there are important differences between *S. fertile* and the Cracow fossil. In the latter, the sporangiophores are described as free from each

* It appears clear, however, that when this is carried out, at least four genera will have to be established, represented by the types *Sphenophyllum Dawsoni*, *S. majus*, *Bowmanites Römeri*, and the strobilus now under consideration.

† "*Bowmanites Römeri*, eine neue Sphenophylleen-Fructification," 'Jahrbuch der K.K. Geolog. Reichsanstalt,' 1895, Band 45, Heft 2, Vienna.

‡ I should have done the same in the case of the strobilus now described, if it had not been for the complete agreement of the axis with that of a *Sphenophyllum*.

§ *Loc. cit.*, p. 241.

‖ *Loc. cit.*, p. 240.

¶ *Loc. cit.*, p. 239.

** *Loc. cit.*, p. 237, Taf. X., fig. 10; *cf.* phot. 13 in the present paper.

†† *Loc. cit.*, p. 239, Taf. X., figs. 4 and 5; *cf.* our Plate 3, figs. 2–5; Plate 1, phot. 7; Plate 2, phot. 10, etc.

‡‡ *Loc. cit.*, p. 233.

other and as seated on the upper surface of the bracts in several concentric circles.* In *S. fertile*, as we have seen, the sporangiophores are the segments of branched appendages; since both dorsal and ventral limbs of the sporophylls are fertile, no bracts are differentiated. It is, of course, possible that in *Bowmanites Römeri* each sporangiophore may represent a branch of a compound ventral appendage, but a comparison based on any such interpretation would be merely speculative.

The *Sphenophyllum Dawsoni* of WILLIAMSON, as will be shown on another occasion, appears to embrace at least two distinct species, one of which is in all probability identical with *S. cuneifolium*, STERNBERG, as M. ZEILLER believed, while the other is not yet certainly identified with any described species, but may not improbably prove to be the fructification of the anatomical form *S. plurifoliatum*, WILLIAMSON and SCOTT, which, again, is very probably referable to *S. myriophyllum*, CRÉPIN. For our present purpose, however, we may continue to speak of the *Sphenophyllum Dawsoni* type.

A comparison of our fossil with *Sphenophyllum Dawsoni* shows that it has less in common with that type of fructification than with *Bowmanites Römeri*. In *S. Dawsoni*, as is well known, each pedicel bears a single pendulous sporangium attached to a "crest" which, no doubt, represents the lamina of the bi-sporangiate species. As the specimens with structure preserved show, there are as a rule two monosporangiate pedicels corresponding to each bract, springing from the ventral surface a little above the base of the gamophyllous verticil. The pairing of the sporangiophores in this type may reasonably be regarded as analogous to the branching of the fertile appendages in *Sphenophyllum fertile*.† The bracts are completely connate for a long distance from their base, and thus differ widely from the appendages of the new cone. Though the two fructifications are extremely divergent in their general morphology, there is a close agreement in certain details of structure. The structure of the pedicel is practically the same in both.‡ As already pointed out the sporangium is attached to the crest in *S. Dawsoni* in quite the same way as it is to the lamina in *S. fertile;* the complex structure of the sporangial wall appears to be essentially the same in both. In fact the agreement in all these features is as close as it could well be, considering that the sporangiophore is monosporangiate in the one case and bisporangiate in the other.

Several other species with monosporangiate pedicels have been described by M. ZEILLER;§ so far as the available data show they present no special points of comparison with our fossil.

* *Loc. cit.*, p. 236.

† *Cf.* BOWER, "Studies in the Morphology of Spore-producing Members, No. V.," 'Phil. Trans.,' B, vol. 196, 1903, p. 231.

‡ *Cf.* WILLIAMSON and SCOTT, *loc. cit.*, p. 938, Plate 85, fig. 57, and see phot. 13, *pd.*, in the present paper.

§ "Étude sur la Constitution de l'Appareil Fructificateur des *Sphénophyllum*," 'Mém. Soc. Géol. de France,' Mem. 11, 1893.

In *Sphenophyllum majus*, BRONN,* the sporangia occur in groups of four, which appear to be inserted at the forks of the dichotomous bracts, thus resembling the synangia of *Tmesipteris*. In the absence of specimens with structure preserved, the exact way in which the sporangia were attached must remain doubtful.

Cheirostrobus presents some remarkable analogies with our cone. In that case, as in *Sphenophyllum fertile*, the sporophylls are only slightly connate at the base, the fertile lobe is branched, bearing, as a rule, three segments or sporangiophores; the bracts, or sterile lobes, are branched in the same way, and much resemble the fertile segments. If we had a *Cheirostrobus* with the dorsal as well as the ventral segments of its sporophylls fertile—a condition which it requires no great stretch of the imagination to picture—we should have a close approximation to the characters of the new strobilus. Though the differences in the anatomy of the axis are, no doubt, decisive against any immediate relationship between the two fructifications, yet, among known Sphenophyllaceous strobili, *S. fertile* stands the nearest to the Burntisland fossil.

The most striking feature in the morphology of *S. fertile* is, no doubt, the fertility and apparent uniformity of all the segments of the sporophyll, whether dorsal or ventral, a condition hitherto without precedent among Pteridophyta. Some analogy may be found in those forms of *Botrychium* in which sporangia are commonly present on the frond or dorsal lobe of the sporophyll,† as well as on the ventral spike. In such cases, however, there is still a marked difference between the frond and the spike, whereas in *Sphenophyllum fertile*, so far as the material allows of a decision, the dorsal and ventral lobes appear to have been perfectly similar to one another, though, with better material, some minor differences between them may possibly be detected.

The question arises whether the fertility of both dorsal and ventral lobes is to be regarded as a primitive or as a derived condition. It must be remembered that *Sphenophyllum fertile* is at present an isolated case; in all other members of its class the dorsal lobes are sterile. In the absence of independent evidence it would be rash to regard the exceptional condition as the original one. On general grounds the other alternative appears the more probable. If we were to assume that the whole sporophyll was fertile from the first, the dorsiventral position of the lobes would be unaccounted for. On the other hand, the advantages of this arrangement are obvious, if we start from the usual condition where the lower lobe is sterile, and exercises a protective function. We may suppose that in the case of *S. fertile* this means of protection had from some cause become superfluous, perhaps because the fertile laminæ

* KIDSTON, "Carboniferous Lycopods and Sphenophylls," 'Trans. Nat. Hist. Soc. Glasgow,' vol. 6 (N. S.), Part I., 1899–1900, p. 128, fig. 25.

† See, for example, A. A. EATON, "Notes on *Botrychium tenebrosum*," 'Rhodora,' vol. 5, p. 275, 1903. The author mentions that in *B. matricariæfolium* a fertile segment of the dorsal lobe usually simulates a miniature spike.

formed by themselves an efficient envelope to the cone, and that hence all the segments of the sporophyll became available for reproductive purposes. On present evidence, therefore, I incline to regard *Sphenophyllum fertile* as a specially modified, rather than as a primitive form of fructification. On this hypothesis it would appear probable that it was derived from a type of strobilus with less differentiation between bracts and sporangiophores than we find in *S. Dawsoni*, or *Bowmanites Römeri*, and rather comparable, in this respect, to the cone of *Cheirostrobus*, where there is a good deal of similarity between the sterile and fertile segments.

There are, however, many details to be cleared up before we have the data for a full discussion of the relations of the new strobilus; any further consideration of the theoretical questions involved will be best postponed until, as we may hope will be the case, additional specimens have come to light. In the meantime it is clear that in *Sphenophyllum fertile* we have a new and distinct type of Sphenophyllaceous fructification.

All the illustrations to this paper, including photographs, drawings, and diagrams, were prepared by my colleague, Mr. L. A. Boodle, to whose skilful aid I am greatly indebted.

EXPLANATION OF PLATES 3–5.

Plates 3 and 4.—Photographs from the sections. In many cases they need to be examined with a lens.

Plate 3.

Phot. 1.—Upper part of the most median longitudinal section. *n.*1, *n.*2, *n.*3, *n.*4 mark the levels of the four nodes shown, numbered from above downwards. Between *n.*2 and *n.*3 a node is obviously missing. *d.l.*, *d.l.*, two dorsal lobes belonging to *n.*1, but detached from the node and cut obliquely. At *n.*2 note the dorsiventral lobing of the left-hand sporophyll, and the relation of the dorsal lobe to the lamina, *lm.* (*cf.* Plate 4, phots. 9 and 10). At *n.*3, on the left, the dorsal and ventral lobes are also clear. *lm.'*, lamina in transverse section, shown in Plate 5, fig. 2. × about 6. S. 2128.*

Phot. 2.—Transverse section, taken above the longitudinal sections. *ax.*, axis, rather compressed; *lm.*, lamina, bearing two sporangia, shown enlarged in phot. 7. × about 5. S. 2130.

Phot. 3.—Transverse section of the axis, showing stele, and part of the outer cortex. The stele shows the solid, triarch primary wood, with the commencement of secondary thickening. × about 50. S. 2134.

Phot. 4.—*sp.l.*, part of a verticil in tangential sections, showing the connate bases

* Number of the section in the author's collection.

of three sporophylls, of which only the dorsal lobes are present. In the two to the right the vascular bundle is seen in each. × about 40. S. 2127.

Phot. 5.—Similar tangential section cutting a verticil further out. The bases of two sporophyll-lobes, *sp.l.*, are shown in transverse section; they are here free from each other. × about 40. S. 2127.

Phot. 6.—Branching lobe of a sporophyll in longitudinal section. *sg.*, *sg.*, the two segments into which the lobe divides. That to the left is cut nearly transversely at the end owing to a bend. × about 40. S. 2127.

Phot. 7.—Lamina (*lm.*) bearing two sporangia (*sm.*, *sm.*); from the transverse section shown in Plate 3, phot. 2, more highly magnified. The sporangium to the left shows its connection with the lamina. × about 20. S. 2130.

Phot. 8.—Part of sporangial wall in surface-view. *st.*, the small-celled stomium, with the buttressed cells of the ordinary wall on either side. Other walls of sporangia appear in section, showing the buttresses well. × 54. S. 2135.

Plate 4.

Phot. 9.—Part of the axis, with node 2 (shown in Plate 1, phot. 1) more highly magnified. As compared with that photograph the right and left are reversed. *sp.*, sporophyll-base on the left; only one lobe, probably the dorsal, is seen; *d.l.*, *v.l.*, dorsal and ventral lobes of the opposite sporophyll. The sporangiophore corresponding to the dorsal lobe is shown in phot. 10. × about 22. S. 2128.

Phot. 10.—From the same section, further to the exterior. The two photographs slightly overlap; the bent dotted line indicates the corresponding parts in each. *lm.*, *lm.*, sporangiferous lamina, bent at an acute angle, and bearing the sporangium, *sm.*, on one side; *pd.*, pedicel of the sporangiophore, lying in the prolongation of the dorsal lobe, *d.l.*, in phot 9. See also Plate 3, phot. 1, *n.*2, on the left. *A*, part of dorsal lobe, or one of its segments, lying between the pedicel and the base of the lobe (see phot. 9). × about 22. S. 2128.

Phot. 11.—Sporangiophore with its sporangia, seen in approximately tangential section cut near the periphery of the cone. *pd.*, pedicel of the sporangiophore in transverse section. *sm.*, one of the two sporangia. *sm.b.*, base of the other sporangium, shown enlarged in phot. 13. *lm.*, *lm'.*, portions of lamina. × about 18. S. 2129.

Phot. 12.—Lamina of sporangiophore, cut almost transversely, immediately below the base of a sporangium, *cf.* the longitudinal section in Plate 5, figs. 3 and 4; in fig. 4 the approximate plane of the transverse section

is marked at 12. Note the great difference in the size of the epidermal cells on the inner and outer faces. *st.*, sharp depression, corresponding to the stomium of the actual sporangium. *v.b.*, vascular bundle. × about 70. S. 2129.

Phot. 13.—Part of the group shown in phot. 11 more highly magnified. *pd.*, pedicel; *v.b.*, its vascular bundle. Below the pedicel the base of one of the sporangia is shown; the cavity at this level is occupied by the internal lining tissue, *i.t.* *l.c.*, *l.c.*, the two large-celled lobes of the sporangial wall. *st.*, the stomium. The wall of the other sporangium is well shown, with buttresses. The approximate plane of this section is marked at 13, in Plate 5, fig. 4. × about 70. S. 2129.

Phot. 14.—Transverse section of another sporangium, cut just above the base. *i.t.*, remains of internal lining tissue; the rest of the cavity is occupied by spores. *st.*, stomium, consisting of small cells, sharply incurved, leaving a narrow crevice. The approximate plane of this section is marked at 14, in Plate 5, fig. 4. × about 40. S. 2129

PLATE 5. Figures from *Camera Lucida* Drawings.

Fig. 1.—Lobe of a sporophyll, seen in an approximately transverse section of the strobilus. The lobe is dividing into four segments, *sg.* 1—*sg.* 4. One of these, *sg.* 3, is only indicated by a slight bulge, and by its vascular bundle, *v.b.* At *v.b.'* the bundle of *sg.* 4 is seen. × 55. S. 2131.

Fig. 2.—Transverse section of a sporangiferous lamina (*lm.'*, in Plate 3, phot. 1), showing the large-celled outer and small-celled inner epidermis. *v.b.*, vascular bundle. × 46. S. 2128.

Fig. 3.—Lamina bearing two sporangia, from a longitudinal section of the strobilus. *lm.*, *lm.*, the lamina; on the left the connection with one of the sporangia is shown in approximately median section. *v.b.*, vascular bundle near base of sporangium; *v.b.'*, vascular bundle near middle of lamina. At *sm.w.*, and elsewhere, the sporangial wall, with its buttresses, is well shown. × 24. S. 2127.

Fig. 4.—Part of the same section more highly magnified, showing the connection between lamina (*lm.*) and sporangium. *v.b.*, vascular bundle seen near its termination; *i.t.*, internal tissue at base of sporangium continuous with mesophyll of lamina; *l.c.*, large-celled region of sporangial wall; *w.*, *w.*, ordinary buttressed cells of wall. Numerous spores are shown. The lines numbered 12, 13, and 14 indicate the approximate planes of the three transverse sections shown in Plate 4, phots. 12, 13, and 14. × 46. S. 2127.

Fig. 5.—Lamina in superficial section passing through the large-celled outer

epidermis. The detached piece at *sm.w.* is no doubt a portion of the wall of one of the sporangia, showing buttressed cells, and at that end of the lamina there are indications of a transition to the sporangial structure. × 46. S. 2134.

Fig. 6.—A. Part of a sporangial wall in transverse section, showing the depressed, small-celled stomium, *st.* On the other cells of the wall the buttresses are seen in sectional or oblique view. This section represents the structure at some distance from the base of the sporangium. × 90. S. 2134.

B. Part of a sporangial wall in section, showing the buttresses, *b*, as seen approximately in surface-view. × 90. S. 2128.

Fig. 7.—Part of a sporangial wall in transverse section, showing the stomium, *st.*, which is here open. *l.c.*, *l.c.*, large cells of the wall on either side, showing that this section was cut near the base of the sporangium. *Cf.* Plate 4, phots. 13 and 14. × 90. S. 2129.

Figs. 8–12.—Spores.

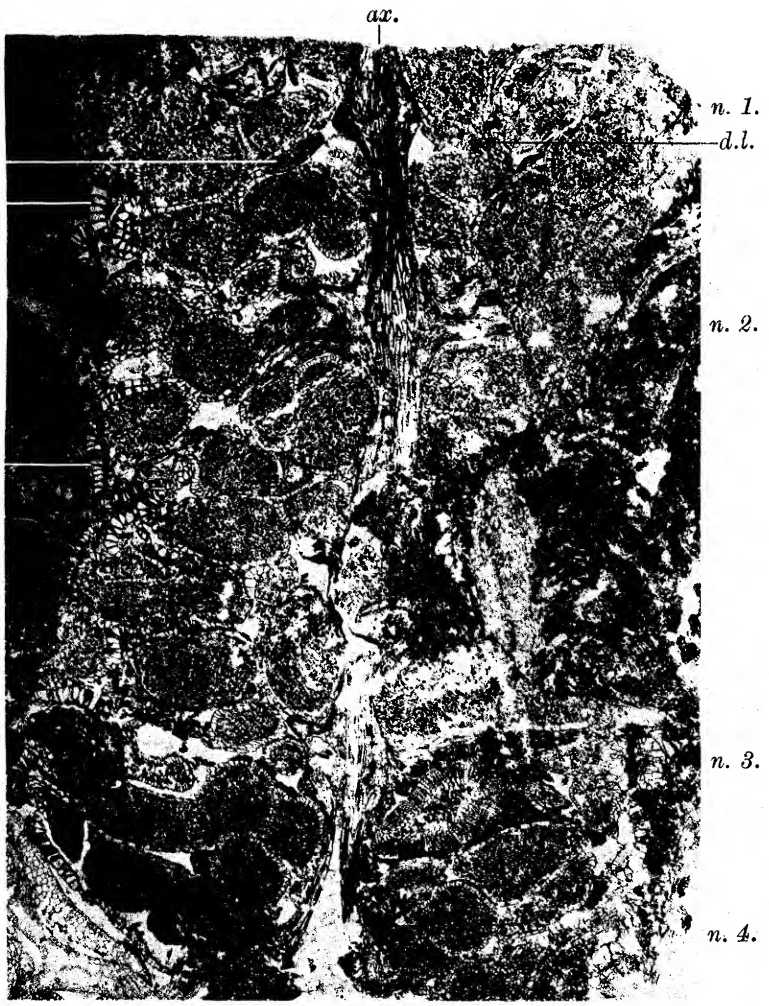
Fig. 8.—Spore in somewhat tangential and obliquely longitudinal section; *ex.*, exospore, seen partly in surface-view; *cr.*, *cr.*, crests of exospore, in section. On the left one crest is partly seen in surface-view; *en.*, contracted endospore. The straight median line is not a septum, but merely a fold of the contracted endospore. × 390 S. 2127.

Fig. 9.—Spore in approximately transverse section, showing the crests, *cr.*, in sectional view. × 390. S. 2134.

Fig. 10.—Spore in longitudinal section, parallel to the crests, *cr.*, which are here seen in surface-view; *ex.*, exospore; *en.*, contracted endospore. × 390. S. 2127.

Fig. 11.—Spore in superficial aspect, showing the crests, *cr.*, running longitudinally in approximately parallel lines. × 390. S. 2130.

Fig. 12.—Section slicing off the extreme outside of the exospore, showing five crests, two of which anastomose. Only a small part of the exospore bearing the crests is present. × 390. S. 2127.



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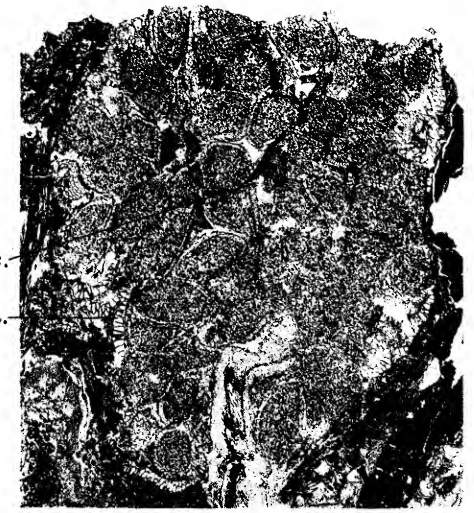

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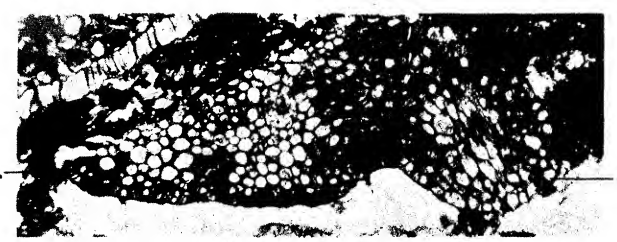

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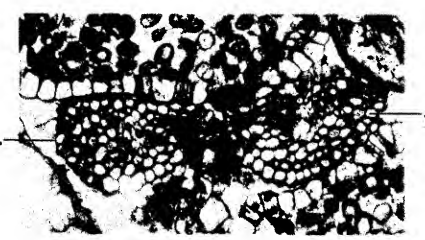

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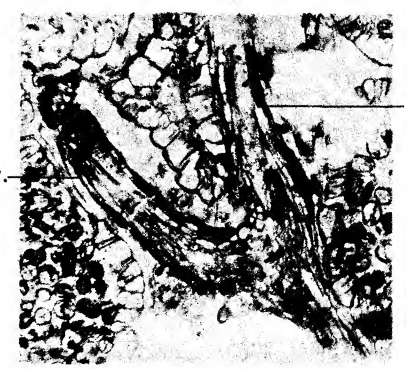

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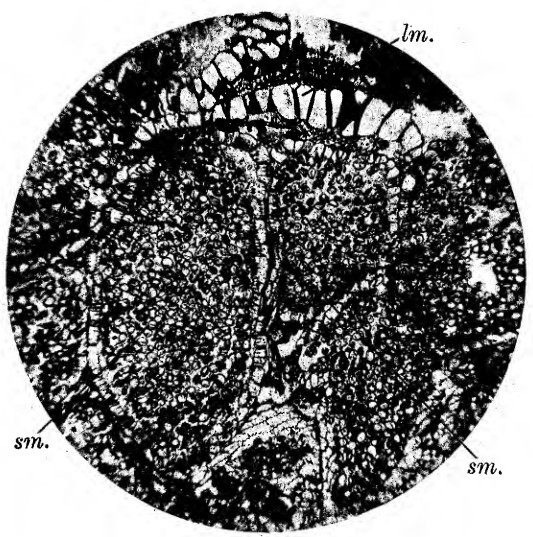

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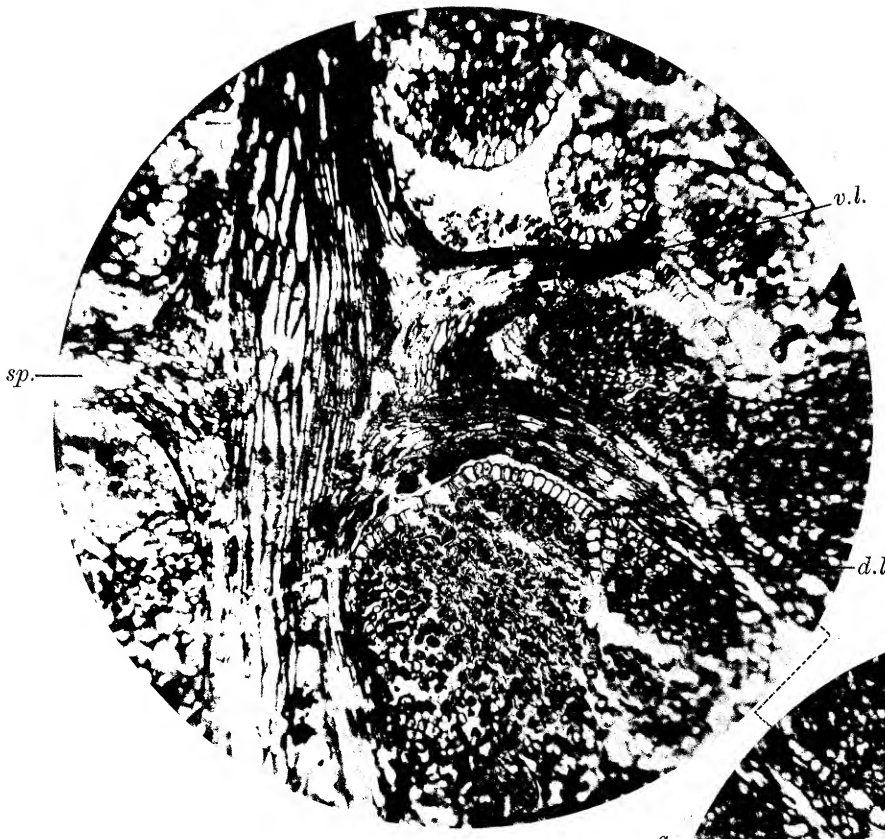
8

L.A.B. PHOT.

SCOTT. SPHENOPHYLLUM FERTILE.



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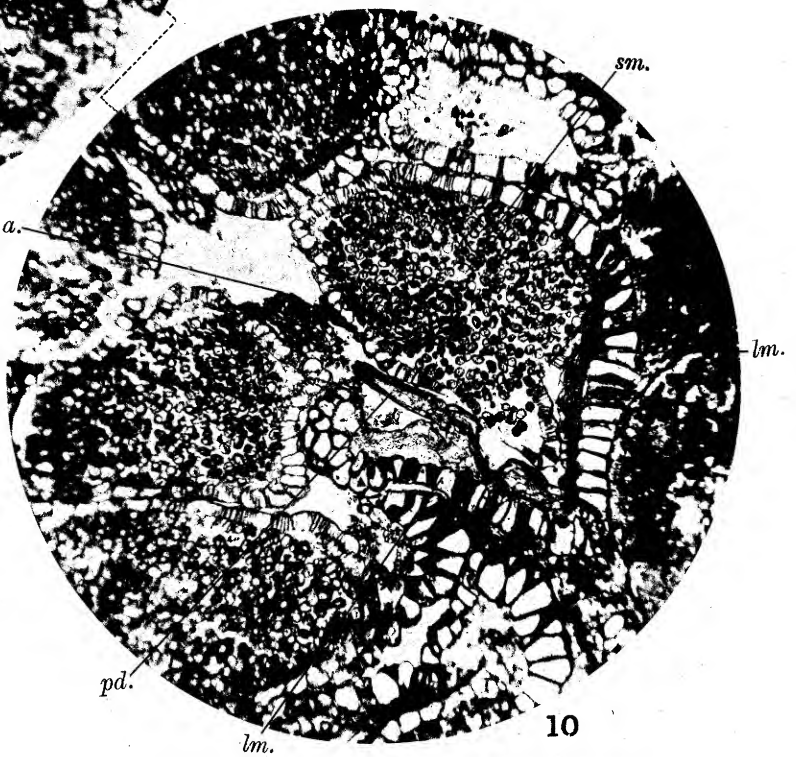

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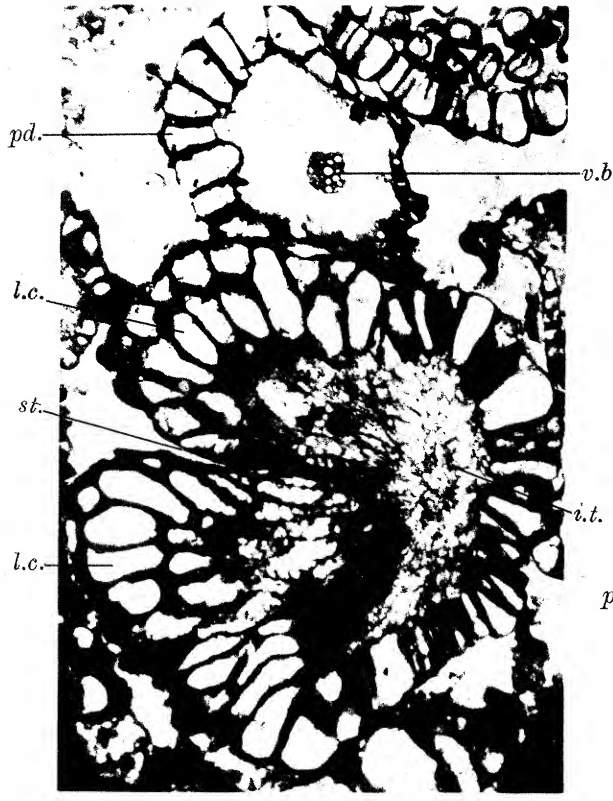

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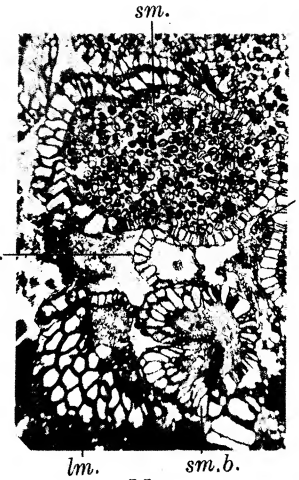

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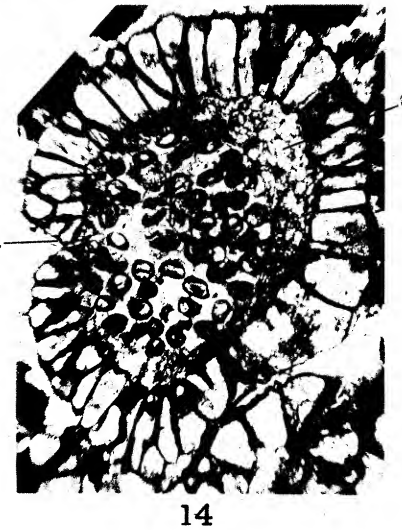

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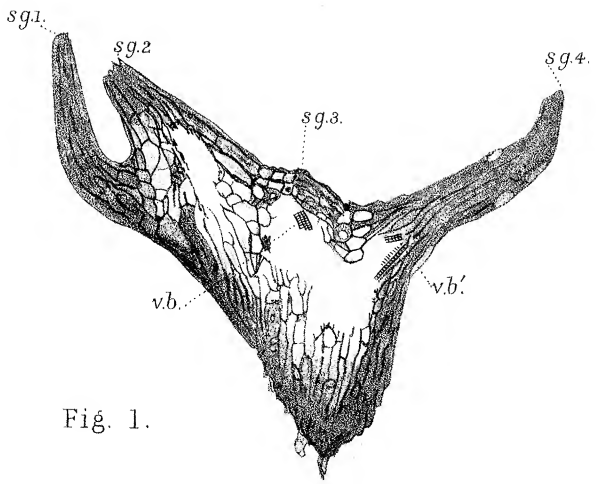
SCOTT. SPHENOPHYLLUM FERTILE.

L.A.B. PHOT.



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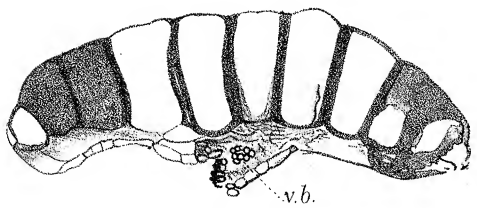


Fig. 2.

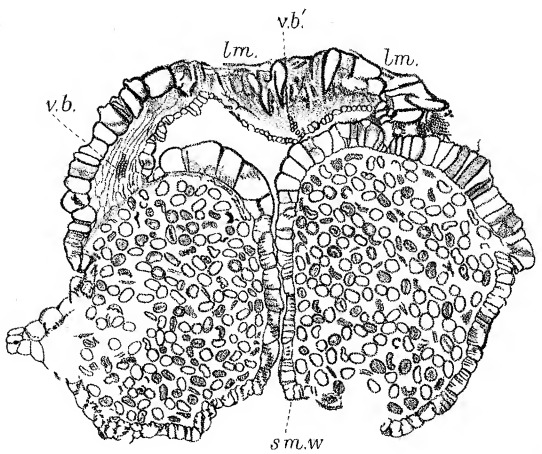


Fig. 3.

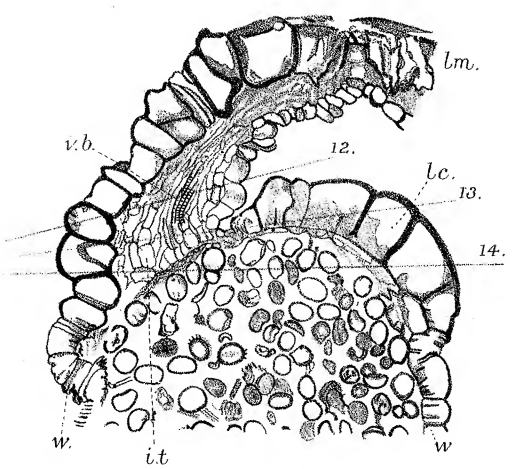


Fig. 4.

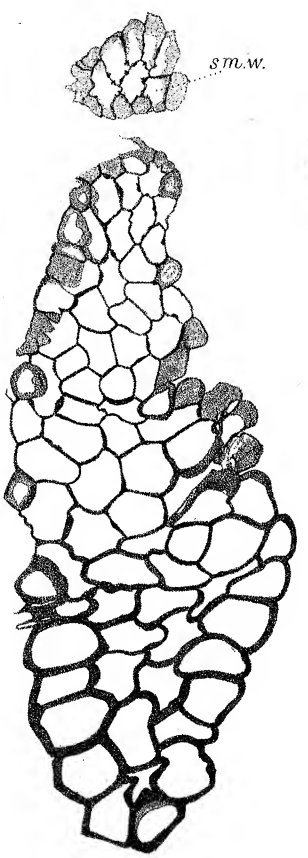


Fig. 5.

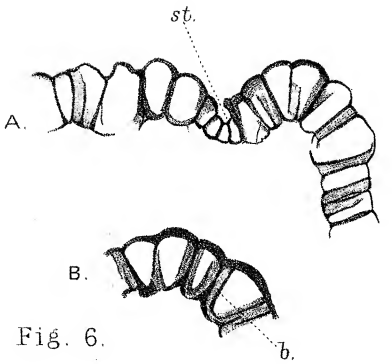


Fig. 6.

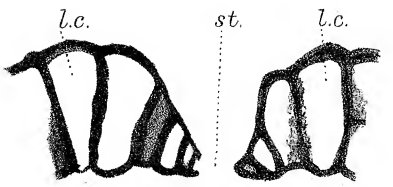


Fig. 7.

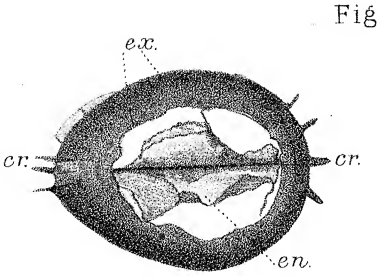


Fig. 8.

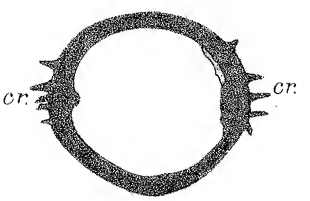


Fig. 9.

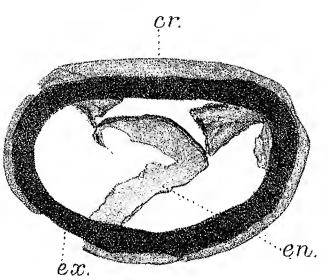


Fig. 10.

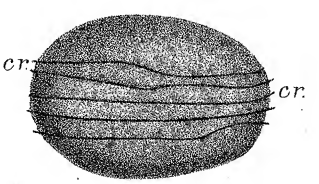


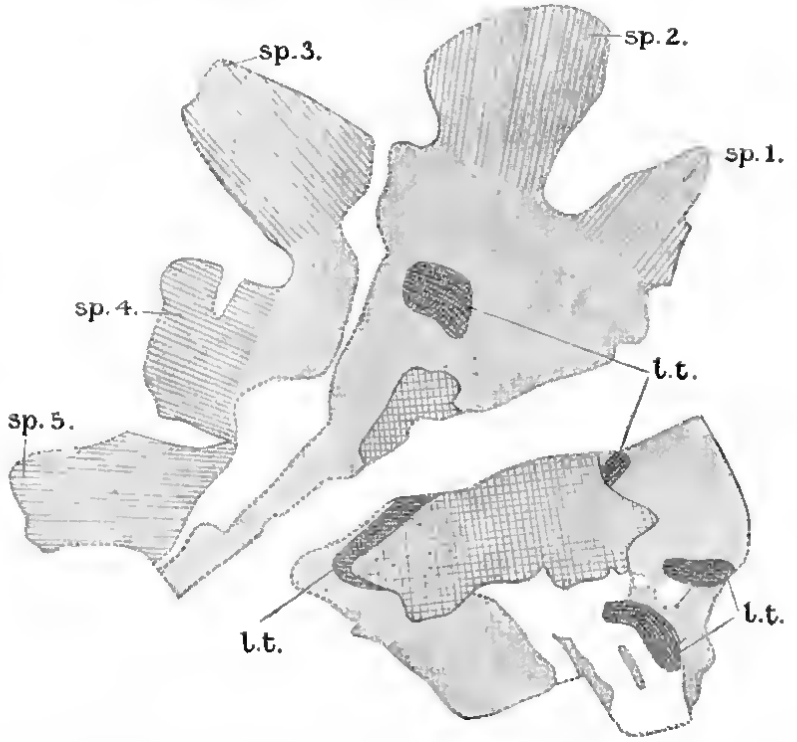
Fig. 11.

Fig. 12.

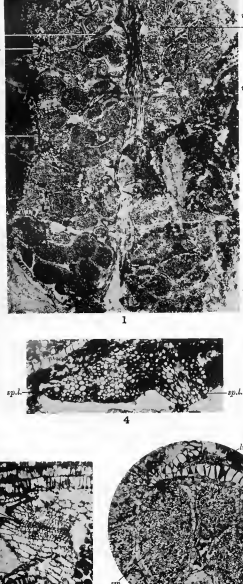
L.A.B. del.

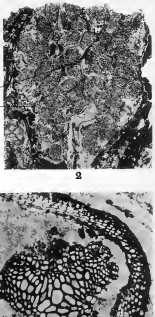
Huth, lith. et imp.

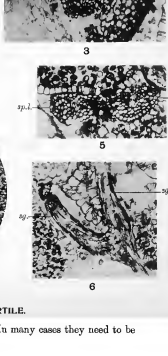
SCOTT — SPHENOPHYLLUM FERTILE.

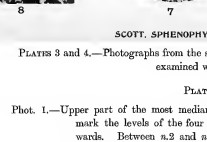


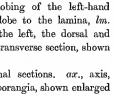
Text-fig. 1.—Transverse section of the axis through a node. The xylem of the stele is shown cross-hatched; the wide crack passes through it. Five leaf-traces (*l.t.*) are shown, two of which are in connection with the stele; *sp.* 1—*sp.* 5, bases of five sporophylls attached to the axis. *Camera lucida* drawing; only the shading is diagrammatic. × 35. S. 2138.

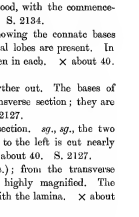


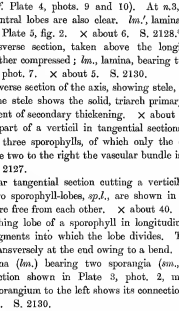


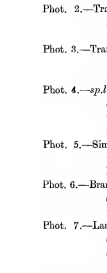












PLATES 3 and 4.—Photographs from the sections. In many cases they need to be examined with a lens.

PLATE 3.

Phot. 1.—Upper part of the most median longitudinal section. *n.*1, *n.*2, *n.*3, *n.*4 mark the levels of the four nodes shown, numbered from above downwards. Between *n.*2 and *n.*3 a node is obviously missing. *d.l.*, *d.l.*, two dorsal lobes belonging to *n.*1, but detached from the node and cut obliquely. At *n.*2 note the dorsiventral lobing of the left-hand sporophyll, and the relation of the dorsal lobe to the lamina, *lm.* (*cf.* Plate 4, phots. 9 and 10). At *n.*3, on the left, the dorsal and ventral lobes are also clear. *lm.'*, lamina in transverse section, shown in Plate 5, fig. 2. × about 6. S. 2128.*

Phot. 2.—Transverse section, taken above the longitudinal sections. *ax.*, axis, rather compressed; *lm.*, lamina, bearing two sporangia, shown enlarged in phot. 7. × about 5. S. 2130.

Phot. 3.—Transverse section of the axis, showing stele, and part of the outer cortex. The stele shows the solid, triarch primary wood, with the commencement of secondary thickening. × about 50. S. 2134.

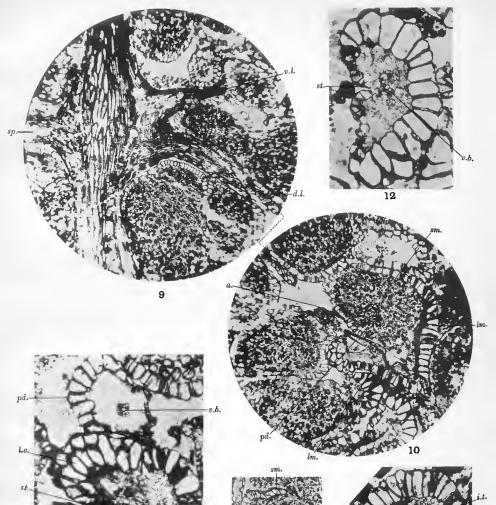
Phot. 4.—*sp.l.*, part of a verticil in tangential sections, showing the connate bases of three sporophylls, of which only the dorsal lobes are present. In the two to the right the vascular bundle is seen in each. × about 40. S. 2127.

Phot. 5.—Similar tangential section cutting a verticil further out. The bases of two sporophyll-lobes, *sp.l.*, are shown in transverse section; they are here free from each other. × about 40. S. 2127.

Phot. 6.—Branching lobe of a sporophyll in longitudinal section. *sg.*, *sg.*, the two segments into which the lobe divides. That to the left is cut nearly transversely at the end owing to a bend. × about 40. S. 2127.

Phot. 7.—Lamina (*lm.*) bearing two sporangia (*sm.*, *sm.*); from the transverse section shown in Plate 3, phot. 2, more highly magnified. The sporangium to the left shows its connection with the lamina. × about 20. S. 2130.

Phot. 8.—Part of sporangial wall in surface-view. *st.*, the small-celled stomium, with the buttressed cells of the ordinary wall on either side. Other walls of sporangia appear in section, showing the buttresses well. × 54. S. 2135.



SCOTT. SPHENOPHYLLUM FERTILE.

PLATE 4.

Phot. 9.—Part of the axis, with node 2 (shown in Plate 1, phot. 1) more highly magnified. As compared with that photograph the right and left are reversed. *sp.*, sporophyll-base on the left; only one lobe, probably the dorsal, is seen; *d.l.*, *v.l.*, dorsal and ventral lobes of the opposite sporophyll. The sporangiophore corresponding to the dorsal lobe is shown in phot. 10. × about 22. S. 2128.

Phot. 10.—From the same section, further to the exterior. The two photographs slightly overlap; the bent dotted line indicates the corresponding parts in each. *lm.*, *lm.*, sporangiferous lamina, bent at an acute angle, and bearing the sporangium, *sm.*, on one side; *pd.*, pedicel of the sporangiophore, lying in the prolongation of the dorsal lobe, *d.l.*, in phot 9. See also Plate 3, phot. 1, *n.*2, on the left. *A*, part of dorsal lobe, or one of its segments, lying between the pedicel and the base of the lobe (see phot. 9). × about 22. S. 2128.

Phot. 11.—Sporangiophore with its sporangia, seen in approximately tangential section cut near the periphery of the cone. *pd.*, pedicel of the sporangiophore in transverse section. *sm.*, one of the two sporangia. *sm.b.*, base of the other sporangium, shown enlarged in phot. 13. *lm.*, *lm'.*, portions of lamina. × about 18. S. 2129.

Phot. 12.—Lamina of sporangiophore, cut almost transversely, immediately below the base of a sporangium, *cf.* the longitudinal section in Plate 5, figs. 3 and 4; in fig. 4 the approximate plane of the transverse section is marked at 12. Note the great difference in the size of the epidermal cells on the inner and outer faces. *st.*, sharp depression, corresponding to the stomium of the actual sporangium. *v.b.*, vascular bundle. × about 70. S. 2129.

Phot. 13.—Part of the group shown in phot. 11 more highly magnified. *pd.*, pedicel; *v.b.*, its vascular bundle. Below the pedicel the base of one of the sporangia is shown; the cavity at this level is occupied by the internal lining tissue, *i.t.* *l.c.*, *l.c.*, the two large-celled lobes of the sporangial wall. *st.*, the stomium. The wall of the other sporangium is well shown, with buttresses. The approximate plane of this section is marked at 13, in Plate 5, fig. 4. × about 70. S. 2129.

Phot. 14.—Transverse section of another sporangium, cut just above the base. *i.t.*, remains of internal lining tissue; the rest of the cavity is occupied by spores. *st.*, stomium, consisting of small cells, sharply incurved, leaving a narrow crevice. The approximate plane of this section is marked at 14, in Plate 5, fig. 4. × about 40. S. 2129

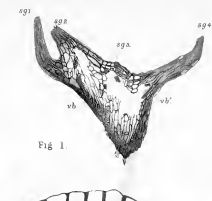


Fig. 1.

Fig. 2.

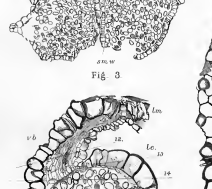


Fig. 3

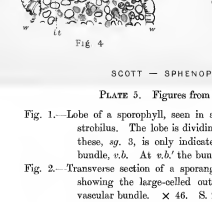


Fig. 4

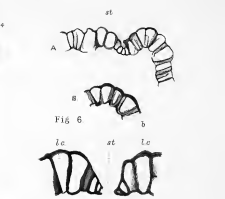


Fig. 6

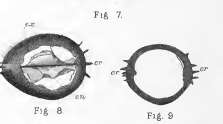


Fig. 7.

Fig. 8

Fig. 9

Fig. 10.

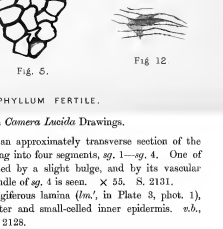


Fig 11

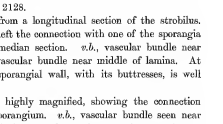


Fig 12

PLATE 5. Figures from *Camera Lucida* Drawings.

Fig. 1.—Lobe of a sporophyll, seen in an approximately transverse section of the strobilus. The lobe is dividing into four segments, *sg.* 1—*sg.* 4. One of these, *sg.* 3, is only indicated by a slight bulge, and by its vascular bundle, *v.b.* At *v.b.'* the bundle of *sg.* 4 is seen. × 55. S. 2131.

Fig. 2.—Transverse section of a sporangiferous lamina (*lm.'*, in Plate 3, phot. 1), showing the large-celled outer and small-celled inner epidermis. *v.b.*, vascular bundle. × 46. S. 2128.

Fig. 3.—Lamina bearing two sporangia, from a longitudinal section of the strobilus. *lm.*, *lm.*, the lamina; on the left the connection with one of the sporangia is shown in approximately median section. *v.b.*, vascular bundle near base of sporangium; *v.b.'*, vascular bundle near middle of lamina. At *sm.w.*, and elsewhere, the sporangial wall, with its buttresses, is well shown. × 24. S. 2127.

Fig. 4.—Part of the same section more highly magnified, showing the connection between lamina (*lm.*) and sporangium. *v.b.*, vascular bundle seen near its termination; *t.t.*, internal tissue at base of sporangium continuous with mesophyll of lamina; *l.c.*, large-celled region of sporangial wall; *w.*, *w.*, ordinary buttressed cells of wall. Numerous spores are shown. The lines numbered 12, 13, and 14 indicate the approximate planes of the three transverse sections shown in Plate 4, phots. 12, 13, and 14. × 46. S. 2127.

Fig. 5.—Lamina in superficial section passing through the large-celled outer epidermis. The detached piece at *sm.w.* is no doubt a portion of the wall of one of the sporangia, showing buttressed cells, and at that end of the lamina there are indications of a transition to the sporangial structure. × 46. S. 2134.

Fig. 6.—A. Part of a sporangial wall in transverse section, showing the depressed, small-celled stomium, *st.* On the other cells of the wall the buttresses are seen in sectional or oblique view. This section represents the structure at some distance from the base of the sporangium. × 90. S. 2134.

B. Part of a sporangial wall in section, showing the buttresses, *b*, as seen approximately in surface-view. × 90. S. 2128.

Fig. 7.—Part of a sporangial wall in transverse section, showing the stomium, *st.*, which is here open. *l.c.*, *l.c.*, large cells of the wall on either side, showing that this section was cut near the base of the sporangium. *Cf.* Plate 4, phots. 13 and 14. × 90. S. 2129.

Figs. 8–12.—Spores.

Fig. 8.—Spore in somewhat tangential and obliquely longitudinal section; *ex.*, exospore, seen partly in surface-view; *cr.*, *cr.*, crests of exospore, in section. On the left one crest is partly seen in surface-view; *en.*, contracted endospore. The straight median line is not a septum, but merely a fold of the contracted endospore. × 390. S. 2127.

Fig. 9.—Spore in approximately transverse section, showing the crests, *cr.*, in sectional view. × 390. S. 2134.

Fig. 10.—Spore in longitudinal section, parallel to the crests, *cr.*, which are here seen in surface-view; *ex.*, exospore; *en.*, contracted endospore. × 390. S. 2127.

Fig. 11.—Spore in superficial aspect, showing the crests, *cr.*, running longitudinally in approximately parallel lines. × 390. S. 2130.

Fig. 12.—Section slicing off the extreme outside of the exospore, showing five crests, two of which anastomose. Only a small part of the exospore bearing the crests is present. × 390. S. 2127.